

A CULTURE STUDY OF *CAULACANTHUS USTULATUS* (CAULACANTHACEAE, GIGARTINALES, RHODOPHYTA) FROM EUROPE AND ASIA.

Jan RUENESS

Department of Biology, Section for Marine Botany, University of Oslo, Norway

ABSTRACT — *Caulacanthus ustulatus* (Turner) Kützinger was collected near Roscoff on the north coast of western Brittany and isolated into unialgal culture. The species is a recent introduction in this area, and the nearest known locality before 1986 was Biarritz. Two other *Caulacanthus* isolates were studied in culture and compared with the Roscoff isolate. One came from Gibraltar, not far from the type locality (Cádiz), and the other was from Qingdao, China, where the alga is passing under the name *C. okamurai* Yamada. The three isolates were morphologically similar, and thus supporting the recent proposal of reducing *C. okamurai* to synonymy with *C. ustulatus*. The isolate from China remained vegetative in culture, while the European isolates produced tetrasporangia. Germination of tetraspores and mature male and female plants are described for the Roscoff isolate. Only one carposporophyte was produced, and the germination of carpospores is described. Vegetative growth was measured on a temperature gradient growth table. Very little growth took place at 6° C. Growth was best at ca. 17° C, and slightly reduced at 13° C and 26° C.

RÉSUMÉ — *Caulacanthus ustulatus* (Turner) Kützinger a été récolté près de Roscoff, sur la côte nord de Bretagne occidentale et conservé en culture unialgale. L'espèce, d'introduction récente dans cette région, n'était, jusqu'en 1986, pas signalée au nord de Biarritz. Deux autres souches de *Caulacanthus* ont été isolées en culture et comparées à celles de Roscoff, l'une de Gibraltar près de la localité-type (Cadix), l'autre de Qingdao en Chine. Les trois isolats sont morphologiquement identiques, y compris le spécimen chinois habituellement désigné sous le nom de *C. okamurai*. Ceci suggère la possible synonymie de *C. ustulatus* et *C. okamurai*, hypothèse déjà retenue par certains auteurs. La souche chinoise est demeurée végétative en culture tandis que les deux souches européennes ont produit des tétraspores. Le développement des tétraspores ainsi que les thalles mâles et femelles sont décrits pour la souche de Roscoff. Un seul carposporophyte a été obtenu. Le développement des carpospores est décrit. Le taux de croissance en fonction de la température a été étudié ; il est faible à 6° C, ■ est optimum à 17° C, légèrement réduit à 13° C et à 26° C.

KEY WORDS: red algae, *Caulacanthus*, Rhodophyta, culture, reproduction, distribution

INTRODUCTION

The first find of the small red alga *Caulacanthus ustulatus* (Turner) Kützinger on the north coast of western France was recently reported by Rio & Cabioch (1988). The alga was growing intertidally in the vicinity of oyster beds near Carantec. This part of the

Brittany coast is probably the most thoroughly investigated with respect to littoral biota as a result of the activities at the Station Biologique, Roscoff. Hence, it is unlikely that the alga has previously been overlooked. The closest site where *Caulacanthus ustulatus* has been collected is Biarritz, in the Bay of Biscay, about 600 km further south. This was the species' known northern limit on the Atlantic coast before 1986. The recent find extends its range so far northwards that it suggests that it may have been introduced, rather than have dispersed northwards along the Atlantic coast of France. It is possible that oysters have acted as the dispersal agent and that the origin of the alga was either southern France or some other remote locality. There has been a marked increase in the number of introduced Japanese species in European waters since the 1960s, mainly due to human activities such as aquaculture and shipping (Ribera & Boudouresque, 1995). One example is *Lomentaria hakodatensis* Yendo, a species of Japanese origin unknown in European waters before it was recently reported from the Roscoff area by Cabioch & Magne (1987).

C. ustulatus was originally described by Turner (1809) on the basis of specimens collected by Clemente at Cádiz, in southern Spain, and lectotypified by Searles (1968). The alga has been reported from warm temperate and tropical West Africa (Lawson & John, 1982; Wynne, 1986a), and along European Atlantic coast from southern Spain (Seoane-Camba, 1965), to Portugal (Ardre, 1970), north Spain (Casares, 1989; Perez-Cirera, 1975) and Biarritz (Feldmann & Hamel, 1937). It is present on the Atlantic islands of Madeira (Levring, 1974), the Azores (Schmidt, 1931; South & Tittley, 1986; Neto, pers. comm.) and the Canary Islands (Børgesen, 1927; Kristiansen *et al.*, 1993), but has not been found in the western Atlantic (Wynne, 1986b). In the Mediterranean Sea there are many records under the name *C. ustulatus*, but as suggested by Augier & Boudouresque (1971), many of these may be based on misidentification of the very similar alga *Feldmannophycus rayssiae* (Feldmann & Feldmann) Augier & Boudouresque. In the northeast Pacific, Dawson (1961) first reported the alga from Baja California, Mexico, and it has later been recorded as common and widespread in Washington and British Columbia (Norris & Wynne, 1968; Scagel, 1973; Gabrielson & Scagel, 1989), but apparently nowhere in between. In the Indian Ocean and east Pacific Ocean the situation is complicated by the fact that similar species have been described under various names. On the basis of morphological and anatomical comparisons of type material with field and cultured specimens, West & Calumpong (1990) concluded that isolates from the Philippines, North Queensland, Australia (as *C. indicus* Weber-van Bosse) and Korea (identified as *C. okamurai* Yamada, 1933) belonged to one and the same species. The Philippine isolate and the Australian isolate were interfertile, whereas the Korean isolate remained vegetative in culture. West & Calumpong (1990) reduced these taxa to synonymy with *C. ustulatus*.

One discrepancy between the Japanese taxon *C. okamurai* and *C. ustulatus* from Europe lies in the pattern of spore development. In *C. okamurai*, Kamura (1963) described a pattern of development that he termed "immediate gelidial type", and which was unlike that reported by Feldmann (1938) for tetraspores of *C. ustulatus* collected near Alger in Algeria. No culture study of *C. ustulatus* from European waters has been undertaken, the life history has not been demonstrated and spermatangial structures not observed.

In this study, cultured isolates of *C. ustulatus* from Roscoff and from Qingdao, China (identified as *C. okamurai*, according to Tseng, 1983) were compared in an attempt to clarify the relationships between the entity of recent origin in the Roscoff area and the alga from Asia. In addition, an isolate from Gibraltar (ca. 100 km east of the type locality Cádiz) was included in the study.

MATERIAL AND METHODS

Field observations were made during a research visit to the Station biologique, Roscoff, in September–November 1993, and the alga was isolated into culture. In June 1994, I collected *Caulacanthus* at Qingdao, China, during the fifth International Phycological Congress. The only species of *Caulacanthus* reported from China and Korea is *C. okamurae* according to Tseng (1983) and Lee & Kang (1986), respectively. The alga was transported live to the laboratory in Oslo, Norway, and isolated into unialgal culture. In March 1996, *C. ustulatus* was isolated from Gibraltar and unialgal cultures were established. In addition living material was received from the Azores, kindly provided by Ana Isabel Neto, but attempts to grow this isolate were unsuccessful. All specimens were found growing in the littoral zone where the alga forms a short turf (1–3 cm) usually attached to rocks and shells. The alga is inconspicuous, but easily recognized by the attenuated, recurved to spine-like axes, each terminated by an obliquely dividing apical cell. Only vegetative specimens were recorded in field collections, and the initial unialgal cultures were established from apical cuttings. Later, tetrasporangia were produced in culture in the isolates from Roscoff and Gibraltar, whereas the isolate from China has remained vegetative. Stock cultures were kept at 12° C and 17° C. They received a light quantity of ca. 30 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ under a 16:8 light:dark regime. The culture medium was IMR/2 (Eppley *et al.*, 1967) adjusted to a salinity of 30 psu. Growth responses at various temperatures were determined for the Roscoff isolate by incubating apical cuttings (1.5 mm) at four temperatures $\pm 1^\circ \text{C}$ (6.3° C; 13.4° C; 17.1° C; 25.6° C) on a temperature gradient growth table. Two Petri dishes, each containing 5 apices, were placed at each temperature and under the same light regime as above. The medium was replenished weekly and individual lengths were measured. The growth experiment was terminated after 7 weeks and results were documented photographically.

RESULTS

Vegetative morphology

The three isolates were morphologically similar and in accordance with earlier descriptions of the species. The isolate from Gibraltar was examined particularly carefully, in view of the possibility of confusion with the Mediterranean species *Feldmannophycus rayssiae*. Figure 1 is a cross-section of this isolate showing two periaxial cells arising from the central axial cell. In Fig. 2, the row of axial cells is seen in a partial longitudinal section. Axial cells are usually 4–6 times longer than broad (ca. 15 μm in diameter). This distinguishes the species from *Feldmannophycus rayssiae*, in which the axial cells are two times longer than broad, and up to 60–70 μm in diameter (Feldmann & Feldmann, 1960). Another distinguishing feature according to Feldmann & Feldmann (1960) and Augier & Boudouresque (1971) is that, in *F. rayssiae*, each axial cell only forms one periaxial cell.

In all isolates of *C. ustulatus*, branches became attached to the substratum by elongation and division of subcortical cells which formed characteristic erumpent attachment pads (Fig. 3). Each erect branch terminated in a distinctive obliquely dividing apical cell.

Reproductive structures

In both the European isolates, tetrasporangia were produced after about three months in culture at 17° C but not at 12° C, whereas the isolate from China has remained vegetative despite attempts to induce the formation of reproductive structures by varying the photoperiod, light intensity, temperature, etc. It is therefore not known whether this isolate is a tetra-sporophyte or a gametophyte. Tetrasporangia are formed in the cortical layer where there are deeply staining sporangial initial cells (Fig. 4). Mature sporangia are zonately divided and measure 30 x 55 µm.

Spermatangia form superficial sori near the branch tips (Fig. 7), where cortical cells cut off 2-3 spermatangial mother cells which in turn cut off spermatangia (Fig. 6). Fertile female plants bear carpogonial branches near branch tips where the supporting cells are intercalary cells close to the axial filament. The carpogonial branches are three-celled and straight (Fig. 9), with the trichogynes penetrating the cortical layer to the surface of the thallus. Details of post-fertilization processes were not studied. Carposporophyte development was seen in only one culture (Roscoff isolate) of mixed male and female plants, and resulted in only one mature cystocarp. Carpospores were released and isolated, but these have not yet produced mature tetrasporophytes. Attempts to cross the Roscoff and Gibraltar isolates have been initiated, but have not so far resulted in carposporophyte development, either in the self-crosses or in the out-crosses. Apparently, fertilization and carposporophyte development do not easily occur in culture (as in the field), and may require a longer period of time than 4 months.

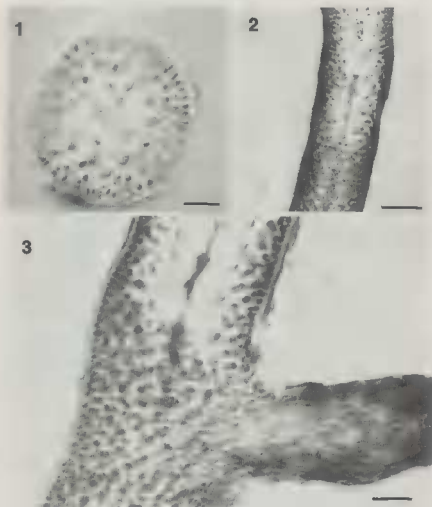
Germination of spores

Tetraspores often germinated on the surface of the thallus. They are variable in size, but measure roughly 25 µm in diameter. A group of germinating tetraspores is shown in Fig. 11. The first division splits the spore into two unequal daughter cells, the smaller of which often gives rise to a rhizoid while the other cell continues to divide into smaller cells within the original spore. There are frequently two rhizoids and two groups of upper cells resulting from an initial partitioning into four cells, two basal cells forming rhizoids and two upper cells that continue to divide and give rise to two more or less separated groups of cells (Fig. 11).

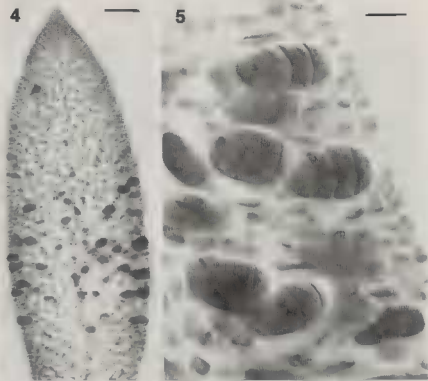
Carpospores were formed only once during this study (Roscoff isolate). A group of germinating carpospores is shown in Fig. 10. Carpospores are variable in size ca. 30 µm in diameter which is slightly larger than tetraspores. Carpospore germination pattern seems to differ somewhat from that of tetraspores. In carposporelings, rhizoids were rarely formed and the germings appear like a single group of cells forming a disc that later gives rise to an upright thallus.

Growth at various temperatures

From Fig. 12 it is seen that very little growth took place at the lowest temperature tested ca. 6° C and best growth occurred at ca. 17° C and somewhat reduced at 13° C and 26° C.



Figs 1-3. *Caulacanthus ustulatus*. Fig. 1. Cross-section of young branch showing axial cell with pit-connections to two periaxial cells (Gibraltar isolate). Scale bar = 30 μm . Fig. 2. Axis in surface view and partial longitudinal section to show cortex and axial filament (Gibraltar isolate). Scale bar = 50 μm . Fig. 3. Part of a branch forming attachment pad (Qingdao isolate). Scale bar = 100 μm .



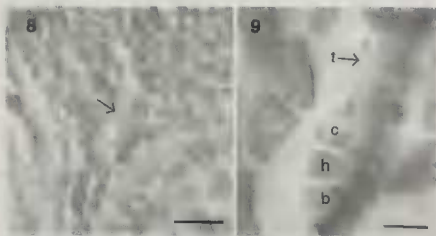
Figs 4-5. *Caulacanthus ustulatus*. Fig. 4. Apical portion of tetrasporic plant showing deeply staining sporangial initials (Gibraltar isolate). Scale bar = 100 μ m. Fig. 5. Section of thallus with mature, zonately divided tetrasporangia (Roscoff isolate). Scale bar = 50 μ m.

DISCUSSION

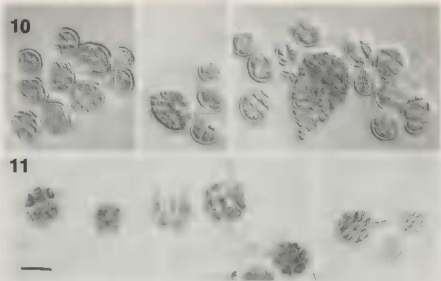
Caulacanthus ustulatus was collected for the first time on the north coast of western Brittany in December 1986 (Rio & Cabioch, 1988). This find represented a substantial change in the known northern limit of the species on the European Atlantic coast. During field work in the vicinity of Roscoff in September-November 1993, the alga was found to be relatively common in many localities, but always in a vegetative state. Rio & Cabioch (1988) suggested that vegetative reproduction was its only means of propagation in this area. Reproductive specimens, especially fertile gametophytes, seem to be very rare in this species and male plants were undescribed from European coast before this study. Bornet & Thuret (1876) were the first to describe the carpogonial branch and some of the post-fertilization stages in material from Biarritz. Searles (1968), who studied the genus in detail, concluded that at least two other Atlantic species were probable synonyms



Figs 6-7. *Caulacanthus ustulatus* (Roscoff isolate). Fig. 6. Transverse section of thallus showing part of spermatangial sorus. Scale bar = 10 μ m. Fig. 7. Branch tip of male plant with extensive spermatangial sorus. Scale bar = 100 μ m.



Figs 8-9. *Caulacanthus ustulatus* (Roscoff isolate). Fig. 8. Longitudinal section of female branch bearing carpogonial filaments (arrow). Fig. 9. Detail of 3-celled, straight carpogonial filament. b. basal cell; h. hypogynous cell; c. carpogonium with trichogyne (t). Scale bar = 10 μ m.



Figs 10-11. *Caulacanthus ustulatus* (Roscoff isolate). Sporelings developed at 17° C. Fig. 10. Germinating carpospores, rhizoids are rarely formed. Fig. 11. Germinating tetraspores. Note formation of rhizoids. Scale bar = 25 μ m.

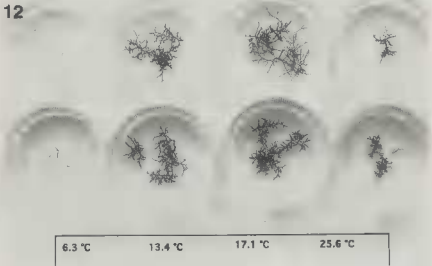


Fig. 12. *Caulacanthus ustulatus* (Roscoff isolate). Growth yield after 50 days in culture at various temperatures and given 30 μ mol photons $\text{m}^{-2} \text{s}^{-1}$ under a 16:8 light:dark regime.

with *C. ustulatus*: *C. rigidus* Kützinger, based on material from Senegal, and *C. divaricatus* (Suhr) Papenfuss from South Africa. Searles (1968) provided detailed descriptions of vegetative and reproductive morphology, including male structures in specimens from South Africa. The present study fully corroborates the descriptions provided by Searles (1968).

As to *Caulacanthus* from the Pacific, Searles (1968) included *C. spinellus* (Hooker et Harvey) Kützinger from New Zealand in *C. ustulatus*. *Caulacanthus indicus* Weber-van Bosse and *C. okamurae* were synonymized with *C. ustulatus* by West & Calumpong (1990) on the basis of morphological and anatomical comparisons of type material with field and cultured specimens. Unfortunately, they provided no illustrations of the algae examined. These authors successfully crossed an isolate from the Philippines (referred to *C. indicus*) with an isolate from North Queensland, Australia (as *C. okamurae*). An isolate from Korea (as *C. okamurae*) was also used, but this remained vegetative in culture, as did the isolate from China used in the present study. In the latest revision of the check-list of marine algae of Japan (Yoshida *et al.*, 1995), *C. okamurae* is reduced to synonymy with *C. ustulatus*.

The claim by Kamura (1963) that the pattern of tetraspore germination in *C. okamurae* differs from that reported for *C. ustulatus* by Feldmann (1938) was examined. There can be no doubt that the illustrations in Kamura (1963) are in good accordance with observations of tetraspore germination in the Roscoff isolate. The formation of one or two rhizoids at an early stage, and the frequent division of germlings into two cell groups were typical features. However, the interpretation of this pattern by Kamura (1963) as an "immediate gelidial type" is misleading, since the characteristic evacuation of the original spore found in the Gelidiales does not occur in *Caulacanthus*. The carpospores seem to have a slightly different mode of development. Rhizoids are rare and division into two distinct cell groups was never seen. Carposporelings were more disc-like than tetrasporelings. The illustrations by Feldmann (1938) show a germination pattern similar to the *Dumontia* type, in which the spore is divided into two more or less equal halves by a wall perpendicular to the substratum. Further divisions take place within the original spore wall to form a hemispherical mass of small cells. The most important difference between spore germination as described by Feldmann (1938) and that reported here is that rhizoids apparently did not bud off in the sporelings studied by Feldmann (1938). This difference is of less importance than the more fundamental difference between the gelidial type and that described for *Caulacanthus*. Furthermore, there is a possibility that the alga studied by Feldmann (1938) belonged to *Feldmannophycus rayssiae*, since Perret-Boudouresque & Sériol (1989) excluded records of *C. ustulatus* from the Algerian flora. Further studies of *F. rayssiae* are required.

In conclusion, the present study supports earlier suggestions that *C. ustulatus* is to be considered as a species of cosmopolitan distribution in warm temperate and tropical waters. Its poor growth at 6°C suggests that its northern growth limit lies in northern France and southern England in the Atlantic and in British Columbia on the north-east Pacific coast. The apparent low frequency of sexual reproduction suggests effective vegetative propagation, probably by fragmentation and reattachment. Since *Caulacanthus ustulatus* from southern Europe is morphologically indistinguishable from *C. ustulatus* from Japan and China, the origin of the Roscoff isolate cannot be determined. Molecular genetic methods may help to resolve the problem. Such investigations are now under way, and a crossability test should be undertaken when fertile gametophytes of both the Pacific and the Atlantic isolates become available.

ACKNOWLEDGEMENTS — I am indebted to the Director and staff of the Station Biologique, Roscoff for providing laboratory and field-collecting facilities, and in particular to Dr Jaqueline Cabioch for information on *Caulacanthus* and her kind advice. Ana Isabel Neto kindly sent specimens from the Azores. Partial financial support was provided by the Norwegian Research Council and the University of Oslo Support Programme.

REFERENCES

- ARDRE F., 1970 — Contribution à l'étude des algues marines du Portugal. *Portugaliae Acta Biologica (B)*, 10 (1-4): 1-423, pls. 1-56.
- AUGIER H. & BOUDOURESQUE C.-F., 1971 — Découverte des cystocarpes de *Feldmannophycus rayssiae* (J. Feld. et G. Feld.) nov. gen. (Rhodophycées, Gigartinales). *Bulletin de la Société phycologique de France* 16: 25-30.
- BØRGESSEN F., 1927 — Marine algae from the Canary Islands especially from Tenerife and Gran Canaria. III Rhodophyceae. Part I. Bangiales and Nemationales. *Det kongelige Danske Videnskabernes Selskab. Biologiske Meddelelser* 6 (6): 1-97.
- BORNET E. & THURET G., 1876 — *Notes algologiques*. Fasc. 1, Paris, 70 p., 25 pls.
- CABIOCH J. & MAGNE F., 1987 — Première observation du *Lomentaria hukodatensis* (Lomentariaceae, Rhodophyta) sur les côtes françaises de la Manche (Bretagne occidentale). *Cryptogamie Algologie* 8: 41-48.
- CASARES C.P., 1989 — Catalogo de la flora bentónica marina de la costa de Guipuzcoa. *Bulletin du Centre d'Etudes et de Recherches Scientifiques de Biarritz* 15: 83-118.
- DAWSON Y., 1961 — Marine red algae of Pacific Mexico. Part 4. Gigartinales. *Pacific Naturalist* 2: 191-343.
- EPPLEY R.W., HOLMES R.W. & STRICKLAND J.D.H., 1967 — Sinking rates of marine phytoplankton measured with a fluorometer. *Journal of experimental Marine Biology and Ecology* 1: 191-208.
- FELDMANN J., 1938 — Sur le développement des tétraspores du *Caulacanthus ustulatus* (Mertens) Kützting (Rhodophyceae). *Bulletin de la Société d'Histoire naturelle de l'Afrique du nord, Alger* 29: 298-303.
- FELDMANN J. & FELDMANN G., 1960 — Une nouvelle Rhodophycée méditerranéenne *Caulacanthus* (?) *rayssiae* sp. nov. *Bulletin of the Research Council of Israel* 10 D: 59-65.
- FELDMANN J. & HAMEL G., 1937 — Floridées de France VII. Gélidiales. *Revue Algologique* 9: 85-140.
- GABRIELSON P.W. & SCAGEL R.F., 1989 — The marine algae of British Columbia, northern Washington, and southeast Alaska: division Rhodophyta (red algae), class Rhodophyceae, order Gigartinales, families Caulacanthaceae and Plocamiaceae. *Canadian Journal of Botany* 67: 1221-1234.
- KAMURA S., 1963 — On the tetraspore-germination of *Caulacanthus okamurai* Yamada. *Bulletin of Arts & Sciences, Division Ryukyu (Mathematical & Natural Sciences)* 6: 73-79.
- KRISTANSEN A., NIELSEN R. & PEDERSEN P.M., 1993 — An annotated list of marine algae collected on Lanzarote, Canary Islands, January 1986. *Courier Forschungsinstitut Senckenberg* 159: 93-102.
- LAWSON G. W. & JOHN D. M., 1982 — The marine algae and coastal environment of tropical West Africa. *Beihefte zur Nova Hedwigia* 70: 1-455.
- LEE I. K. & KANG J. W., 1986 — A check list of marine algae in Korea. *Korean Journal of Phycology* 1: 311-325.
- LEVRING T., 1974 — The marine algae of the archipelago of Madeira. *Boletim do Museu Municipal do Funchal* 28: 5-111.

- NORRIS R.E. & WYNNE M.J., 1968 — Notes on marine algae of Washington and southern British Columbia. III. *Synopsis* 1: 133-146.
- PERRET-BOUDOURESQUE M. & SERIDI H., 1989 — *Inventaire des algues marines benthiques d'Algérie*. Marseille, GIS Posidonie publication, pp. 1-117.
- PÉREZ-CIRERA J.L., 1975 — Catalogo florístico de las algas bentónicas de la Ria de Corme y Laga, NO de España. *Anales del Instituto Botánico Antonio José Cavanilles* 32: 5-87.
- RIBERA M.A. & BOUDOURESQUE C.-F., 1995 — Introduced marine plants, with special reference to macroalgae: mechanisms and impact. *Progress in Phycological Research* 11: 187-267.
- RIO A. & CABIOCH J., 1988 — Apparition du *Caulacanthus ustulatus* (Rhodophyta, Gigartinales) dans la Manche Occidentale. *Cryptogamie Algologie* 9: 231-234.
- SCAGEL R.F., 1973 — Marine benthic plants in the vicinity of Bamfield, Barkley Sound, British Columbia. *Synopsis* 6: 127-145.
- SEARLES R.B., 1968 — Morphological studies of red algae of the order Gigartinales. *University of California Publications in Botany* 43: 1-86.
- SEOANE-CAMBA J., 1965 — Estudios sobre las algas bentónicas en la costa sur de la Península Ibérica (litoral de Cádiz). *Investigacion Pesquera* 29: 1-216.
- SCHMIDT O.C., 1931 — Die marine Vegetation der Azoren in ihren Grundzügen dargestellt. *Bibliotheca botanica* 102: 1-116.
- SOUTH G.R. & TITTLE I., 1986 — *A checklist and distributional index of the benthic marine algae of the North Atlantic Ocean*. Huntsman Marine Laboratory and British Museum (Natural History), St Andrews & London, 76 p.
- TSENG C.K. (ed.), 1983 — *Common seaweeds of China*. Beijing, Science Press, 316 p., pls 1-149.
- TURNER D., 1809 — *Fuci sive plantarum fucorum generi a botanicis ascriptarum icones descriptiones et historia*. Vol. II., London, J. & A. Arch, 162 p., pls 72-134.
- WEST J.A. & CALUMPONG H.P., 1990 — New records of marine Algae from the Philippines. *Micronesica* 23: 181-190.
- WYNNE M.J., 1986a — Report on a collection of benthic marine algae from the Namibian coast (southwestern Africa). *Nova Hedwigia* 43: 311-355.
- WYNNE M.J., 1986b — A checklist of benthic marine algae of the tropical and subtropical western Atlantic. *Canadian Journal of Botany* 64 (10): 2239-2281.
- YAMADA Y., 1933 — Notes on some Japanese algae V. *Journal of the Faculty of Science, Hokkaido Imperial University, Series V, Botany*, 2 (3): 277-285.
- YOSHIDA T., YOSHINAGA K. & NAKAJIMA Y., 1995 — Check list of marine algae of Japan. *Japanese Journal of Phycology (Sôrui)* 43: 115-171.